

VARIATION IN THE *BERLANDIERA PUMILA* (ASTERACEAE) COMPLEX

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ABSTRACT

Plants from southeast Texas and adjacent Louisiana previously identified in part as *Berlandiera* \times *betonicifolia* are regarded here as geographical variants of *B. pumila* and are treated as *B. pumila* var. *scabrella* Nesom & Turner, var. nov. Variety *pumila* and var. *scabrella* differ in features of cauline and foliar vestiture, that of the upper leaf surfaces allowing the most consistent separation. The type collection of *B. betonicifolia* (Hook.) Small (*Silphium betonicifolium* Hook., 1835) represents a species distinct from *B. pumila* and comprises plants previously identified by the name *B. texana* DC. (1836), which is displaced by the former. While the morphology of *B. pumila* var. *scabrella* has suggested that it originated as a hybrid between typical *B. pumila* and *B. betonicifolia*, there is no evidence of current hybridization between these two species.

KEY WORDS: *Berlandiera*, *B. pumila*, *B. betonicifolia*, Asteraceae

RESUMEN

Plantas del sudeste de Texas y la parte adyacente de Louisiana identificadas previamente en parte como *Berlandiera* \times *betonicifolia* son consideradas aquí como variantes geográficas de *B. pumila* y son tratadas como *B. pumila* var. *scabrella* Nesom & Turner, var. nov. La variedad *pumila* y var. *scabrella* difieren en características del indumento caulinar y foliar, siendo la del haz la que permite una mejor separación. El tipo de *B. betonicifolia* (Hook.) Small (*Silphium betonicifolium* Hook., 1835) representa una especie distinta de *B. pumila* y comprende plantas previamente identificadas como *B. texana* DC. (1836), que es desplazada por la anterior. Mientras que la morfología de *B. pumila* var. *scabrella* ha sugerido que se formó como un híbrido *B. pumila* típica y *B. betonicifolia*, no hay evidencia de hibridación actual entre estas dos especies.

Shinners (1951) followed Small (1903, 1933) in treating *Berlandiera pumila* (Michx.) Nutt. as a species restricted to the southeastern United States east

of the state of Mississippi; its vicariad west of the Mississippi River was identified as *B. dealbata* (Torr. & A. Gray) Small. Turner and Johnston (1956) returned to the concept of Torrey and Gray by including the western plants within a more broadly defined *B. pumila*, acknowledging the existence of a distributional hiatus between the two geographic segments of the species. The western segment of *B. pumila* occurs primarily in east Texas and adjacent Louisiana (Fig. 1), barely reaching into the adjacent corners of south-eastern Oklahoma and southwestern Arkansas.

Shinners (1951) accepted the existence of *Berlandiera betonicifolia* (Hook.) Small as a distinct species similar to western *B. pumila* (*B. dealbata* in his sense) in morphology and geography. Turner and Johnston (1956) viewed *B. betonicifolia* as intergrading with both *B. pumila* and *B. texana* DC. and adopted the earlier combination *B. texana* var. *betonicifolia* (Hook.) Torr. & A. Gray. This group of entities/taxa is referred to in the present study as

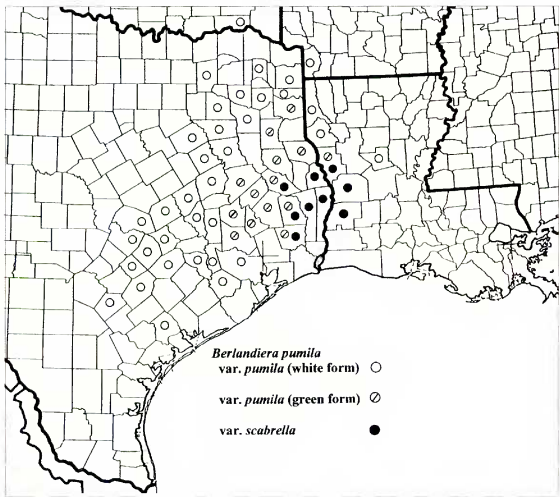


FIG. 1. Distribution by county of *Berlandiera pumila* in Texas, Louisiana, Arkansas, and Oklahoma.

the "*B. pumila* complex."

In a biosystematic study of the whole genus, Pinkava (1967) found that crosses between all combinations of species of *Berlandiera* were easily made under greenhouse conditions and he provided evidence of natural hybridization between many of the taxa. All entities of the genus are reported to have an apparently invariant chromosome number of $n=15$ (see Pinkava 1970 for original counts and summary of previous literature). Based on the morphology of artificially constructed hybrids, Pinkava observed that "although the [GH] type of *B. betonicifolia* lies between the F_1 [of *B. pumila* and *B. texana*] and *B. texana*, it is definitely an intermediate of the two species and its name has been retained for the hybrid group" (p. 292). Pinkava used the designation "*B. \times betonicifolia*" and has been followed in this by recent treatments that have adopted his view.

Pinkava interpreted the *Berlandiera pumila* complex in east Texas (his Fig. 4, p. 294) essentially as an intergrading nexus between *B. pumila*, *B. betonicifolia*, and *B. texana*. In *B. betonicifolia*, "most characters are intermediate to those of the putative parents in varying degrees and combinations over its range of east-central Texas and western Louisiana" (Pinkava 1970, p. 1625). He found apparent intermediates between *B. texana* and *B. betonicifolia*, however, to be rare. Although his histogram of hybrid index values in the "Western *B. pumila*/*texana* complex" (Fig. 2b, p. 290) indicates that he observed several populations of such intermediates, only one such collection is mapped on his Fig. 4 (1967); it is in central Louisiana (Rapides Parish), where *B. pumila* apparently is absent but where *B. texana* (sensu Pinkava) is known by a number of collections (Fig. 2).

In the Louisiana flora, Gandhi and Thomas (1989) and MacRoberts (1989) recognized both *Berlandiera pumila* and *B. \times betonicifolia*, showing these two taxa with nearly identical geographic ranges. MacRoberts (1989, p. 313) noted that the latter "seems to be inordinately common compared with its putative parents." *Berlandiera pumila* and *B. \times betonicifolia* both have been recognized from the southeastern corner of Oklahoma (Taylor and Taylor 1994).

Berlandiera \times betonicifolia (sensu Pinkava) was reported from the southwestern corner of Arkansas (Miller Co.) by Orzell and Bridges (1987, p. 88), who adopted Pinkava's interpretation of variability among the plants they observed. They noted that "Our specimens mostly fit the putative backcross hybrid of *Berlandiera \times betonicifolia* with *B. pumila*, . . . although some of our specimens have dense, matted white-tomentose pubescence, and could be referred to *B. pumila*." Smith (1994) identified these Arkansas plants simply as *B. pumila*.

Cronquist (1980) did not include *Berlandiera betonicifolia* among the three species formally recognized in his treatment of the genus for the southeastern

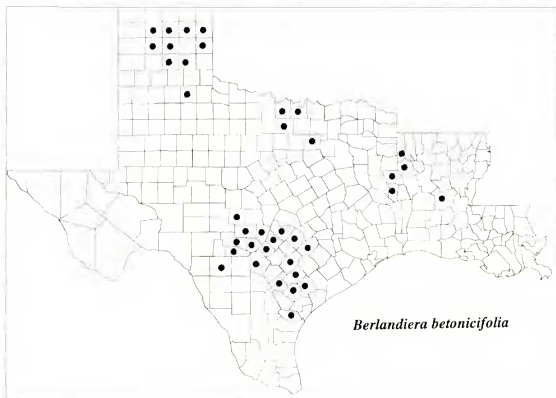


FIG. 2. Distribution by county of *Berlandiera betonicifolia* (see text for definition) in Texas and Louisiana. The species also occurs northward through Oklahoma into northern Arkansas, Missouri, and southern Kansas.

United States. He referred to it in introductory comments simply as the name covering hybrids between *B. pumila* and *B. texana*.

Despite the considerable previous attention given to patterns of variation and accompanying taxonomy of plants of the *Berlandiera pumila* complex in Texas and Louisiana, field experience in east Texas and adjacent Louisiana suggested that the pattern of variation in this group might be viewed from another perspective. This problem was approached in more detail through study of numerous collections available in regional herbaria and field observations in 1996 and 1997 covering Anderson, Angelina, Cherokee, Hardin, Houston, Jasper, Montgomery, Nacogdoches, Newton, Polk, Rusk, Sabine, San Augustine, San Jacinto, Shelby, Trinity, Tyler, Upshur, Van Zandt, Walker, and Wood counties, Texas, and Vernon Parish, Louisiana.

THE IDENTITY OF *BERLANDIERA BETONICIFOLIA*

Pinkava did not examine the original type material of *Silphium betonicifolium*, but based on a photo, he noted (1967, p. 297) that "Drummond's holotype [of *S. betonicifolium*] more closely resembles *B. texana* [than *B. pumila*] and was assigned to it [*B. texana*] as a variety by Torrey & Gray (1842),

who commented that other specimens fitted neither varietal description completely." Gray annotated at least two of the Drummond sheets now at K (see below) as "*Berlandiera texana* DC. f. *betonicifolia* Torr. & Gray." The present examination of the original material at K shows it to be the species that has long been identified as *Berlandiera texana* DC., which de Candolle named a year later than Hooker's *S. betonicifolium*.

The material at K consists of four sheets, which are similar among themselves in habit and other morphological features, and it seems likely that Drummond collected all of this material at the same site. The lectotype (designated below) bears detailed sketches of the ray and disc achenes, which were probably used by Bentham in his preparation of the Compositae treatment for *Genera Plantarum*.

The correspondingly modified nomenclature for this species is summarized below.

***Berlandiera betonicifolia* (Hook.) Small, Fl. SE U.S. 1246, 1340. 1903.**

Silphium betonicifolium Hook., Comp. Bot. Mag. 1:99. 1835. *Berlandiera texana* var. *betonicifolia* (Hook.) Torr. & A. Gray, Fl. N. Amer. 2:281. 1842. *Berlandiera xbetonicifolia* (Hook.) Small sensu Pinkava, Brittonia 19:297. 1967. TYPE: (as cited in the protologue and on the label, see comments in text): [United States, Louisiana], New Orleans, 1833, *T. Drummond s.n.* (LECTOTYPE, designated here: K!; ISOLECTOTYPES: K-3 sheets!; probable ISOLECTOTYPE: GH!). Color photos of two of the K isolectotypes are on file at TEX.

Berlandiera texana DC., Prodr. 5:317. 1836. TYPE: TEXAS: between the Trinity River and Bejar [San Antonio], Jun 1828, *J.L. Berlandier 2044* (HOLOTYPE: G fide!; ISOTYPES: F, MO, NY, P).

On the lectotype of *Silphium betonicifolium* (and one of the isolectotypes), presumably written by Hooker himself, the collection locality and date are given as "N. Orl. 1833." The possible GH type material of *S. betonicifolium* was annotated by B.L. Turner and M.C. Johnston in 1955: "Possible isotype, as questioned by Gray (Fl. N. Amer. 2:281. First edition). Drummond's plant possibly came from Texas—'New Orleans' being a citation error." Gray himself (1842) cited the locality of the type collection as "New Orleans?," apparently questioning its provenance. There are no other historical or recent collections of any species of *Berlandiera* from southeastern Louisiana and none from Mississippi, and it seems unlikely on this basis that Drummond made the "betonicifolia" type collection in the area of New Orleans.

One of the isolectotypes bears a glued annotation label (pasted over the lower stem), presumably in Asa Gray's script: *Berlandiera texana* DC. Torr. Gr. Fl. N. Am. 2.286." At the bottom of the label, in print, there is a line "Jacksonville (Amer. Bor.) Drummond 1833." Gray (presumably) crossed out the word Jacksonville and wrote above it "Louisiana." An early Texas site for "Jacksonville" is not known to the present authors.

Drummond sailed from New Orleans to reach Texas (Brazoria County) in March 1833, and during his 21-month stay in Texas (Geiser 1948), he stayed or traveled in areas where *Berlandiera pumila* var. *pumila* occurs (e.g., Fayette, Austin, Lee, Colorado, Fort Bend counties), but he did not travel in the area where plants previously identified as *B. ×betonicifolia* (see below) occur (Fig. 1). Geiser's account shows that Drummond passed through at least one county (Gonzales Co.) where *B. betonicifolia* (of the present interpretation) is known to occur (Fig. 2). From among the 100 or more collections of the *Berlandiera pumila* complex at LL, TEX, the plant most similar to the Kew types is a collection (*Gentry & Smith 2024*, LL) from Victoria Co., which is only a short distance from Gonzales County.

Considering the information presented in the present study, Drummond probably collected the plants of the type material in south-central Texas at some locality near the Guadalupe River, which traverses both Gonzales and Victoria counties. Drummond collected along this river (fide Geiser) between 24 April and 26 September, 1834, at which time he was assembling his "set II." One of the isolectotypes bears the handwritten notation "Texas II, no No. [s.n.], *Drummond*."

With his last set of collections, Drummond sailed from New Orleans in December 1834 on his return to Europe. He disappeared enroute (apparently in Cuba) but his specimens arrived safely.

THE NATURE OF *BERLANDIERA BETONICIFOLIA*

Berlandiera betonicifolia (*B. texana* of previous interpretations) occurs from panhandle and south-central Texas and adjacent Louisiana (Fig. 2) northward through Oklahoma into northern Arkansas, Missouri, and southern Kansas (Pinkava 1967; Turner and Johnston 1956; Great Plains Flora Assoc. 1986). This species can be separated from the *B. pumila* complex without intergrades by making comparisons in the key below. Collections of both *B. betonicifolia* and *B. pumila* have been made in the same counties in central and east Texas (Victoria, Bastrop, Burleson, Gonzales, Travis, Fayette, and Shelby) and parishes of adjacent Louisiana (Caddo and DeSoto) (Figs. 1 and 2), but in this region of geographic overlap, there are no plants suggestive of hybridization and/or introgression between them. For the most part, plants that previously have been interpreted as such hybrids (*B. pumila* var. *scabrella*, as identified here) occur outside of the present geographic range of *B. betonicifolia*.

As noted by Pinkava (1967), the lower stems of plants of *Berlandiera betonicifolia* from parts of Texas tend to be silky-pilose with soft, white hairs while those from further north have shorter, thicker, and slightly vitreous hairs. Intraspecific variation in leaf shape and margin also exists within the species, but this variability apparently does not bear on its relationship to *B. pumila*.

Based primarily on perceived similarities in stem leafiness and leaf insertion, Turner and Johnston (1956) regarded *Berlandiera betonicifolia* (as *B. texana*) and *B. pumila* var. *scabrella* (as *B. betonicifolia*) as conspecific and intergrading. The current study, in contrast, concludes that *B. betonicifolia* is distinct from other closely related entities.

VARIATION WITHIN *BERLANDIERA PUMILA*

Plants from east Texas and western Louisiana previously identified as *Berlandiera pumila* and *B. ×betonicifolia* are best represented as two entities within a single species (*B. pumila*), differing in features of vestiture. The nomenclatural summary for typical *B. pumila* and the newly recognized variant are given here.

Berlandiera pumila (Michx.) Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:342.

1841. *Silphium pumilum* Michx., Fl. Bor.-Amer. 2:146. 1803. TYPE: UNITED STATES. FLORIDA: [no date], *A. Michaux 10* (HOLOTYPE: P fiche!).

Berlandiera tomentosa var. *dealbata* Torr. & A. Gray, Fl. N. Amer. 2:282. 1842. *Berlandiera pumila* var. *dealbata* (Torr. & A. Gray) Trcl., Rep. Ark. Geol. Survey 1888, 4:193. 1891.

Berlandiera dealbata (Torr. & A. Gray) Small, Fl. S.E. U.S. 1246, 1340. 1903. TYPE: UNITED STATES. "ARKANSAS" [present day Oklahoma], [date], *T. Nuttall* (HOLOTYPE: NY fiche!).

Berlandiera pumila (Michx.) Nutt. var. *scabrella* Nesom & Turner, var. nov. TYPE: U.S.A. TEXAS. Jasper Co.: roadside of Hwy 63, 0.8 mi E of jct with FM 1738, 1.0 mi E of crossing of Melholms Creek, 7.0 mi E of jct Hwys 290 and 96 in Jasper; narrow strip of native vegetation along side of hwy, buffer to loblolly pine plantation behind; dominant scrubby post oak, blackjack oak, black hickory, and bluejack oak, with less common sweetgum, dogwood, sassafras, yaupon, buckeye, and winged sumac; *Berlandiera* scattered but abundant along edge of woods for ca 50 yards on N side of hwy, in deep, loose sand; 16 May 1998, *G.L. Nesom 98J1* (HOLOTYPE: TEX; ISOTYPES: ASTC, BRIT, FSU, GH, IBE, LSU, MISSA, MO, NCU, NLU, OKL, SHST, TAES, TAMU, UARK, US, USCH).

A. B. pumilo var. *pumilo* similis sed differt vestimento hispidulo paginis superis foliaribus, trichomatibus basaliter erectis basibus incrassatis.

Most of the variation that occurs among plants of *Berlandiera pumila* is attributable to three patterns: 1) vestiture of the upper leaf surfaces—a relatively abrupt transition in easternmost Texas from fine, thin-based, reclining or appressed hairs to thick, basally erect hairs; 2) vestiture density of the stems and lower leaf surfaces—interpopulational variation in central and east-central Texas and the gradual reduction in density, with loosening of the matted tomentum and shortening and thickening of the hairs, in populations from west to east toward Louisiana; and 3) stem vestiture coloration—production of reddish cross-wall pigments mostly in southeastern Texas and adjacent west-central Louisiana. Each of these patterns is discussed below in more detail.

1) The morphological feature that shows the sharpest geographic transition within *Berlandiera pumila* is the nature of the vestiture on the upper leaf surfaces: fine, silky, thin-based, basally reclining or appressed hairs (var. *pumila*) vs. thicker-based and basally erect hairs (var. *scabrella*). It is primarily on this basis that the taxonomic separation between the varieties of *B. pumila* in the present interpretation can be made most consistently. Intermediacy in hair morphology occurs in Cass, Harrison, Shelby, Polk, and Tyler counties and Caddo and DeSoto parishes (and perhaps others). This feature also was emphasized by Pinkava (1970) in his key to Texas *Berlandiera* and was described by Torrey and Gray (1842, their "*B. tomentosa* y").

2) Plants of *Berlandiera pumila* var. *pumila* with a dense vestiture of long, thin, matted hairs show white stems and distinctly bicolored leaves (white beneath, green above), the stem and lower leaf surfaces obscured by the tomentum (the "white form" of var. *pumila*). Plants with trichomes shortened in length show a corresponding reduction in density of vestiture and the green surfaces of the stems and leaves are visible through the hairs (the "gray-green form" of var. *pumila*, not mapped on Fig. 1, intermediate between the "white form" and "green form"). Shorter trichomes of the lower leaf surfaces tend to be somewhat erect and separate rather than parallel to the surface and closely intertwined. Only the white form of *B. pumila* occurs in populations from the westernmost area of the range (Fig. 1). The white form and gray-green form occur broadly over east Texas. In this area are plants with dense white tomentum as well as plants with vestiture reduced by degrees in density, this feature tending to be relatively uniform within a local population. A corresponding reduction in stem vestiture appears to be the only morphological difference correlated with the variation in leaf vestiture. The "green form" of *B. pumila* occurs in easternmost Texas counties and in Louisiana; in these plants the vestiture is further reduced, with the lower leaf surfaces showing greenish or yellowish-green and hardly different in color from the upper surface. In this area, the gray-green form occurs infrequently and the white form is rare or absent. The reduction in stem and abaxial leaf vestiture is characteristic of some populations of var. *pumila* and all of var. *scabrella*. In the present attempt to characterize finer patterns of infraspecific variation, we note that the informally designated white, gray-green, and green forms are found within var. *pumila* but var. *scabrella* includes only the green form.

3) The stem vestiture of plants from a cluster of southeasternmost Texas counties (Hardin, Polk, Jasper, Newton, Angelina, and Sabine cos.) and adjacent Louisiana (Fig. 1) is reduced and the hairs distinctly colored. The hairs are basally erect, though not thick and long like those of *B. betonicifolia*, and the strongly colored cross-walls of all the hairs give a purplish or reddish-brown color to at least the upper stems. Such purplish stems are char-

acteristic primarily of plants recognized here as var. *scabrella*, but intergradation in this feature occurs with plants of var. *pumila* (the gray-green form) from slightly further west. In these intergrades, hairs with colored cross-walls are formed among the more abundant white hairs but are less noticeable within the predominately grayish cauline vestiture.

The evolutionary origin of *Berlandiera pumila* var. *scabrella*, as suggested by Pinkava (1977), may have been through hybridization between *B. betonicifolia* and typical *B. pumila*. Both *B. betonicifolia* and *B. pumila* var. *scabrella* have reduced vestiture of stems and leaves and neither produces white tomentum; the upper leaf surfaces in both are somewhat hispid with thickened, basally erect hairs. Stem hairs in both entities usually produce purplish cross-walls. As noted above, however, such hybridization is not currently evident and parallel evolution is an equally reasonable explanation of these morphological similarities between *B. betonicifolia* and var. *scabrella*.

THE NATURE OF TYPICAL *BERLANDIERA PUMILA*

Berlandiera pumila in its typical form occurs in western Florida (where the type collection was made by Michaux), Alabama, Georgia, South Carolina, and North Carolina. The general distribution of the species was shown by Pinkava (1967); its absence from Mississippi remains a reality (S. McDaniel, pers. comm.). Various populations of *B. pumila* in this eastern segment of its geographic range correspond to both the "white form" and "green form" of the western segment of the species, as outlined in the comments above. There is no variation within *B. pumila* of the eastern U.S. toward the morphological features characteristic of var. *scabrella*.

KEY TO THE TAXA OF THE *BERLANDIERA PUMILA* COMPLEX

1. Stem hairs thick-based, erect, mostly 1.0–1.5(–2.0) mm long, commonly distinctly flattened and vitreous; lower leaf surfaces greenish; leaves lanceolate to deltate, the mid-cauline and upper usually sessile**B. betonicifolia**
1. Stem hairs soft and thin, densely matted and closely appressed or sometimes oriented in parallel, the length of the individual hairs difficult to observe, sometimes more loosely arranged and less than 1 mm long, white; lower leaf surfaces white to gray-green or greenish; leaves ovate to triangular or lanceolate, the mid-cauline and upper usually on short (1–2 mm) petioles**B. pumila** (2)
2. Upper leaf surfaces softly pubescent with very thin, appressed or basally reclining hairs (sometimes basally erect in Cass, Harrison, and Shelby cos., Caddo Parish), the leaves strongly to weakly or not at all bicolored; stem vestiture relatively dense and matted or reduced in density with the stem surface visible, the hairs evenly whitish or some with purplish cross-walls near the base**B. pumila** var. **pumila**
2. Upper leaf surfaces minutely hispidulous with relatively thicker-based and basally erect hairs, the leaves not bicolored; stem surface visible, the vestiture reduced in density, the hairs often reddish-brown to purple because of colored cross-walls**B. pumila** var. **scabrella**

ACKNOWLEDGMENTS

Specimens have been examined from ASTC, BRIT, NLU, SBSC, SHST, TAES, TAMU, and LL, TEX. The K holotype was loaned to Turner at LL, TEX. Walter Holmes provided information on collections housed at BAYLU and Sidney McDaniel verified the absence of *Berlandiera pumila* from Mississippi. Thanks to Mark Bierner and Reviewer #2 for their helpful criticisms.

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